Environmental and Experimental Botany 68 (2010) 26–30

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Evaluation of hydraulic lift in cotton (*Gossypium hirsutum* L.) germplasm

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ARTICLE INFO

Article history:
Received 17 February 2009
Received in revised form
21 September 2009
Accepted 11 October 2009

Keywords:
Cotton
Roots
Water uptake
ET
Water content

ABSTRACT

Hydraulic lift (HL) in plants is defined as the redistribution of water from wetter to drier soil through the plant roots in response to soil water potential gradients. Water is released from the roots into the dry soil when transpiration is low (night) and reabsorbed by the plant when higher transpiration rates are resumed (daylight). It was hypothesized that since HL is not of sufficient magnitude to meet total transpirational demands, there may be sufficient water transferred to maintain viable roots in the surface soil in anticipation of root water uptake for plant development from rain events before it is lost to water evaporation and/or runoff. Cotton (*Gossypium hirsutum* L.) plants of diverse genetic backgrounds were grown in a split-root container with roots of one plant divided between the two adjacent soil volumes. The soil in one container was allowed to dry while the adjacent soil container remained wet for the duration of the tests. Cotton transpiration was lowered by covering the plant with black cloth for several hours while changes in soil water content were measured in both containers using calibrated soil water sensors. Results showed that water was transferred from the wet to the dry soil through the root system at low transpiration rates. There was also an indication of genetic diversity in the magnitude of HL that may be due to differences in root resistance to water flow since total root length for a particular genotype was either smaller in the dry soil or similar to total root length in the wet soil. The amount of water transferred was small, but when integrated over a soil depth represented an amount ranging from 11% to 32% of corresponding daily evapotranspiration rates of 2–6 mm d^{-1}, respectively, which could presumably maintain root viability for additional root water uptake when made available. These results are important in dryland cotton production where additional transpiration represents increased lint yield and plant breeders may consider this trait in their selection of cotton germplasm with drought resistance.

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1. Introduction

The process whereby soil water is redistributed from wet soil layers deep in the profile to drier soil layers near the soil surface by the root systems of plants is termed hydraulic lift (HL) (Richards and Caldwell, 1987). This phenomenon has been reported to occur in a large number of plant species (Caldwell et al., 1998; Liste et al., 2008). They describe the HL process as the movement of water from the roots to the soil because of root xylem water potential becoming greater than the surrounding soil water potential when transpiration rates are low, i.e., <0.5 mm d^{-1}. In many cases the water that is transferred to the surrounding soil when transpiration is low, usually at night, is reabsorbed by roots the following day to become a portion of the daily transpiration (Caldwell et al., 1998).

Much of the work in HL investigations has been conducted using diverse plant material such as shrubs and trees under field conditions (Moreira et al., 2003). Some studies, however, have indicated that HL does occur in herbaceous species as well (Xu and Bland, 1993; Sekiya and Yano, 2004; Wan et al., 2000; Liste et al., 2008). Laboratory experiments have also been conducted to suggest the potential for HL and to document the extent of the phenomenon (Baker and Van Bavel, 1988). Furthermore, a number of studies have suggested that the occurrence of HL in one plant may benefit neighboring plants by moving water to the drier upper soil layers so that the neighbor plant may have access to the water, provided the neighbor plant has a relatively shallow root system (Sekiya and Yano, 2004). For example, an experiment by Hirota et al. (2004) showed that HL that occurred in a Markhamia (*Markhamia lutea* [Benth.] Schumann) tree successfully transferred sufficient water to neighboring rice (*Oriza sativa* L.) plants and allowed the rice to remain viable during a drying period. In contrast, the rice plants not associated with the tree roots desiccated during the same drying period.

In some cases it has also been suggested that HL can account for a portion of the daily transpirational requirements of the plant. For example, Caldwell et al. (1998) estimated that 20–40% of the daily transpiration might be accounted for by HL. Also, Baker and Van Bavel (1988), demonstrated HL with cotton grown with a split-

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0098-8472/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.envexpbot.2009.10.002

Table 1
Cotton genotypes and origin (race) used for hydraulic lift experiments.

Genotype	Region of adaptation in USA	Pedigree
Acala Maxxa	West	1753 8/S4959
Paymaster HS-26	High plains	Acala SJ-4/5B9-184
Acala SJ-2	West	SJ-1 selection
Deltapine-90	Southeast	DP-6516 and DP6-582
Deltapine-491	Mid-south/South Texas	DP-5415/DP-2156
Fibermax-958	Texas	CS6S/Siokra S-324/Sicala V-i
Stoneville-213	Mid-south	Stoneville 7 selection
TX 63	–	Unadapted race stock
TX 117	–	Unadapted race stock

root system measuring water that was transferred from the wet to the dry soil via the root system. However, they concluded that the amount of water transferred due to HL would not meet the daily transpiration demand.

The importance of HL is magnified for the Texas High Plains, where about 4×10^6 ha per year are under crop cultivation with around 60% dryland and 40% irrigated from the Ogallala aquifer (TWDB, 1997). In this region, about half the rainfall is <10 mm per event (average for Lubbock, Texas; Steve Mauget, personal communication) and the long-term annual rain is 458 ± 146 mm (Lascano, 2000). The 10-mm rain events result in a shallow wetting of the soil surface and water that infiltrates is likely lost to evaporation and thus not contribute to plant transpiration. When this is the case and given the dry and hot conditions that develop, particularly for dryland conditions without the benefit of irrigation, cotton roots in the upper part of the soil profile face the risk of becoming non-functional. However, if HL occurs, the possibility exists for maintaining roots near the soil surface in a functional condition in anticipation of a rain event, giving the plant an opportunity to uptake the water that otherwise is lost to evaporation. The underwritten benefit of HL is to increase seasonal plant transpiration by increasing root water uptake per rain event as a result of viable roots near the soil surface under dryland conditions.

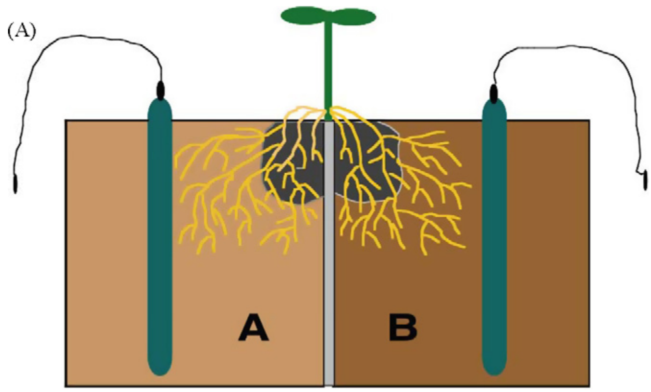
It has been shown that genetic variability exists in the development of the cotton root system in terms of changes in root architecture (McMichael and Quisenberry, 1991). Thus, we hypothesize that differences in HL may also occur that may result in an increase in the ability of some genotypes to maintain viable roots in drier soil. However, to evaluate differences in HL for a wide germplasm pool and on a timely basis, techniques must first be developed and evaluated concerning suitability to separate the germplasm for potential differences in HL. Therefore, the objectives of this study were two-fold: (i) to develop and evaluate a protocol to determine differences in cotton plant HL, and (ii) to collect preliminary data on diversity in HL in selected cotton lines using the developed protocol in the first objective.

2. Materials and methods

2.1. Plant material and cultural conditions

Cotton was used as the test plant and all experiments were conducted at the USDA-ARS Cropping System Research Laboratory in Lubbock, TX. The germplasm selected and used ranged from modern to obsolete cultivars containing some converted race stocks from the National Cotton Germplasm Collection (Percival, 1987) (Table 1). The germplasm was selected on the basis of the region of adaptation and previous studies on early root system development in the case of the race stock entries. Seed of each entry were planted into small peat cups containing ~15–20 g of fritted clay material (All-Sorbs, Van Bavel et al., 1978) and maintained in a well-watered

(A)



(B)

Fig. 1. View of apparatus for measuring hydraulic lift (HL) in cotton. (A) Schematic of cross section of root boxes with (A) indicating dry and (B) indicating wet side of apparatus. Blue rods indicate position of soil water probes. Dark hatched areas indicate original peat cups. (B) View of apparatus with plants growing in greenhouse prior to experiments. For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.

condition at a constant air temperature of 28 °C in a controlled environment chamber. The relative humidity in the chambers ranged from 30% to 35% and the combination fluorescent and incandescent lighting was set for 14 h daylight and 10 h dark. The plants remained in the peat cups for 2–3 weeks after planting (3–4 leaf stage).

Following the initial 2–3-week growth period the root systems of the seedlings were split by separating the roots in the peat cup into two halves. Each half was then transplanted into one of two larger (12 cm L × 22 cm W × 30 cm H) plastic containers filled with local soil (Amarillo fine sandy loam) a predominant soil series in the Texas High Plains (Fig. 1A and B). The soil was packed uniformly to a bulk density of 1.5 g cm^{-3} for a total of 87.2 kg per container. This arrangement is similar to that described by Baker and Van Bavel (1988). The transplanted seedlings were maintained in a well-watered condition and allowed to grow for an additional 2 weeks in the controlled environment chamber prior to being transferred to a greenhouse (7–8 leaf stage). Once in the greenhouse the plants with split-root systems (Fig. 1B) grew for an additional 4 weeks (12–15 leaf stage) prior to the initiation of the measurements. Ten container systems consisting of one plant per two smaller containers (split-root system) of each cotton entry were evaluated. Once the experiment began for each split-root container the soil was allowed to dry in one of the split containers for approximately 1 week prior to covering the plant as suggested by Wan et al. (2000).

2.2. Experimental protocol

Two probes to measure volumetric changes in soil water content (Echo probe, Decagon Devices, Pullman, WA) were placed vertically in each of the split-root containers (Fig. 1A). The probes, 0.15-m in length transversed the entire depth of the container. The probes were attached to a data logger (Campbell Scientific, Model 23X, Logan, UT) that provided both the excitation voltage for the probes

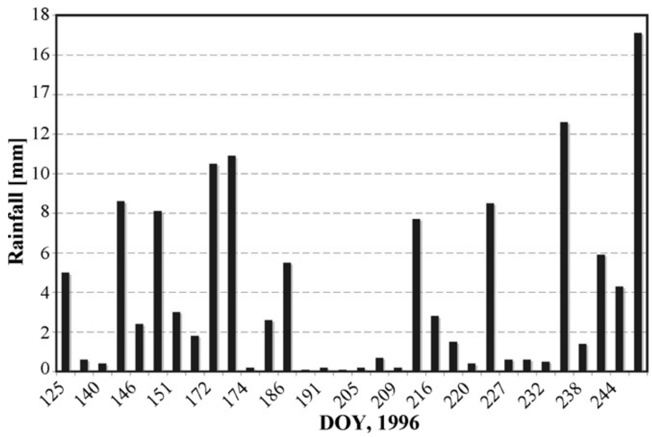


Fig. 2. Rainfall frequency and amount for the 2006-growing season at the Cropping Systems Research Laboratory, USDA-ARS Lubbock, TX.

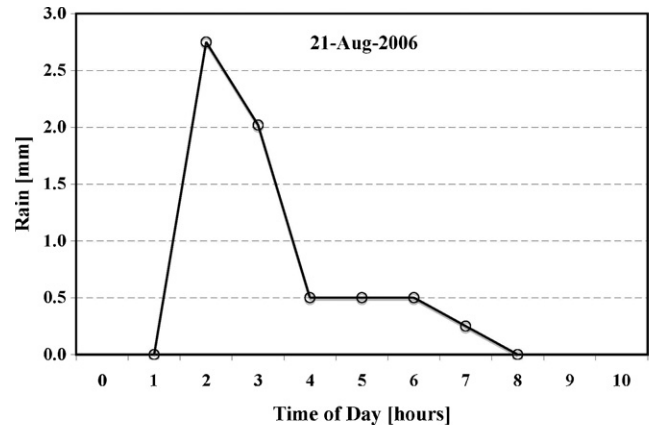


Fig. 3. The development of a single rain event at Lubbock, TX for 21 August 2006, showing the duration and intensity.

and measured their output, which was measured every 10 s and averaged over a 1-min period. Probe outputs were converted to volumetric water content (VWC) using a calibration curve developed for the Amarillo soil that was used to grow the cotton plants (McMichael and Lascano, 2003).

For each cotton plant with a split-root, the soil water content in one of the split-root containers was allowed to dry by withholding water, while the soil in the other half was maintained well watered. When the soil in the non watered side reached a VWC of <5%, the wet compartment was watered and the plant was covered with a black mesh nylon cloth to reduce transpiration and simulate nighttime conditions, following the procedures of Wan et al., 2000. The plant remained covered for approximately 4 h after which the black mesh nylon cloth was removed. The output of the soil water probes in both the wet and dry split-root containers were recorded every 5 min during the measurement period. After these measurements, the roots from each split container were removed by washing the soil from the roots. The total length of roots in each container was measured using the procedure described by Tennant (1975). The total root length of both the wet and dry half of the split-root container of each variety was measured to show differences in root length in each half of the container. There was no normalization of the data to adjust for changes in VWC but rather to show the differences in root length of the different varieties. Also, the contribution of the changes in VWC to transpiration demand across a range of daily evapotranspiration (ET) rates for dryland cotton production in a semiarid environment was calculated.

3. Results

An illustration of rain events that may occur during a growing season at the USDA Cropping Systems Research Laboratory field plots in Lubbock, TX is shown in Figs. 2 and 3. For example, in 2006 rain events from <1 to 11 mm were recorded from 1 May (DOY 122) to 15 August (DOY 228) (Fig. 2). The duration of these rain events was one to two consecutive days at most. It is also noted that the frequency of rain events increased as well as their intensity from 15 August (DOY 228) to 1 September (DOY 245) after the growing season was over. A typical storm event is shown in Fig. 3 for 21 August (DOY 234), which depicts a typical short duration lasting only a few hours with the highest intensity being upwards of 2.7 mm. This information points up the potential significance of the ability of a plant to use HL as a means of maintaining viable roots since the plant would not have sufficient time to grow new roots to take advantage of the short duration, high intensity rain events (Fig. 3).

Examples of HL showing the transfer of water via the root system of a cotton plant for three cotton genotypes from the wet to the dry compartment are illustrated in Fig. 4. The first example (Fig. 4A, Acala Maxxa), shows that prior to adding water to the wet compartment, the soil VWC was 0.186 $m^3 m^{-3}$ and the corresponding soil VWC of the dry compartment was 0.112 $m^3 m^{-3}$. Immediately after adding water to the wet compartment and covering the plant at 7.3 h, the VWC of the soil in the un-watered compartment increased by 1% to 0.123 $m^3 m^{-3}$ as a result of transfer of water due to HL between the two split-root compartments. Even though the increase in VWC is only 1% and when expressed as water depth, i.e., change in VWC multiplied by container depth, $(0.123–0.113) \times 300\,mm = 3.0\,mm$ water in the soil container, it represents a significant amount of water that may impact the daily transpiration. The second example (Fig. 4B, DPL-90) shows a transfer of 1.8 mm of water between the split-root compartments, and the third example (Fig. 4C, TX117), shows a transfer of 3.6 mm of water due to HL. Similar results, as those shown in Fig. 4, were also obtained for other genotypes (Table 1) tested for HL. However, the magnitude of the water transfer response due to HL was not the same for all genotypes tested and differences may indicate genetic variability in root resistance to water flow.

The average measured root length (RL) of both dry and wet split-root compartments of the cotton plants used in the HL experiments are shown in Fig. 5. The measurements showed that RL between the dry and wet split-root compartments were similar with the exception of Paymaster HS-26 and Acala SJ-2. There was considerable range in RL between the cotton varieties evaluated for HL. The RL values ranged from 32 m for Stoneville-213 and 213 m for DPL-491. This wide range in RL's was expected given the genetic differences of the cotton varieties selected for our experiments (McMichael and Quisenberry, 1991).

Water transferred via HL and their potential contribution to three daily ET rates of 2, 4 and 6 mm d^{-1} is shown in Fig. 6 for the different varieties tested. These ET rate values represent the daily range of values commonly measured in dryland cotton production on the semiarid Texas High Plains (Lascano and Baumhardt, 1996). These results indicated that on average, for the cotton genotypes tested, the percent of daily ET that could potentially be derived from HL transfer is 32%, 16% and 11% for the 2, 4 and 6 mm d^{-1} ET rates, respectively. Assuming a linear relationship between cotton lint yield and ET, an increase in ET should correspond to an increase in lint yield. This effect is even more important under dryland conditions where cotton grown in the Texas High Plains is often subjected to frequent droughts and ~1/2 of our rain events are <10 mm d^{-1} (Fig. 1). The inference is that the occurrence of HL could presumably contribute to the maintenance of viable roots near the soil surface

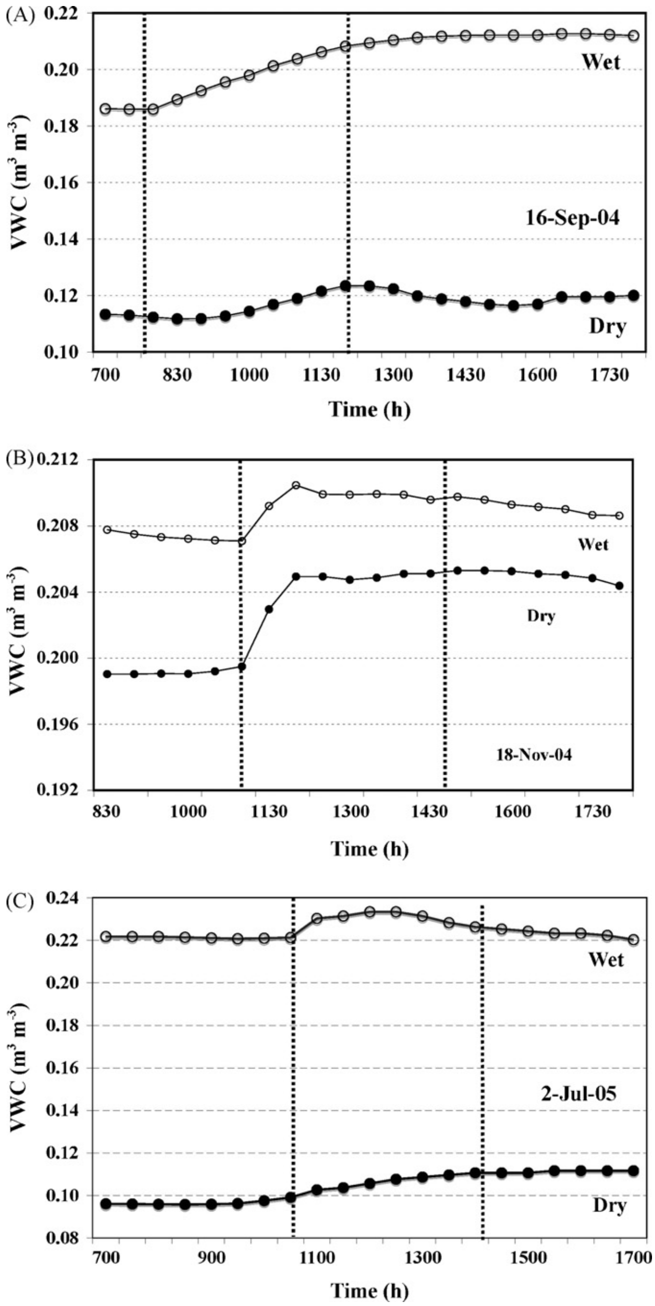


Fig. 4. Examples of time course of changes in soil volumetric water content (VWC) during a hydraulic lift experiment for three cotton genotypes. The solid vertical lines indicate when plants were covered to reduce transpiration while water was added to one of the two split-root compartments. (A) Acala Maxxa; (B) DPL-90; and (C) TX117.

that can then take up water received from these small rain events; otherwise, this water would simply evaporate from the soil surface without contributing to the transpiration of the cotton plant.

4. Discussion

Hydraulic lift occurs in plants when water moves from wet zones lower in the soil profile to upper dry zones in response to water potential gradients and encountered resistances in the soil and across the roots (Baker and Van Bavel, 1988). According to Caldwell et al. (1998) the axial resistance to water movement from the roots should be low in order for water to move from the roots to the dry soil.

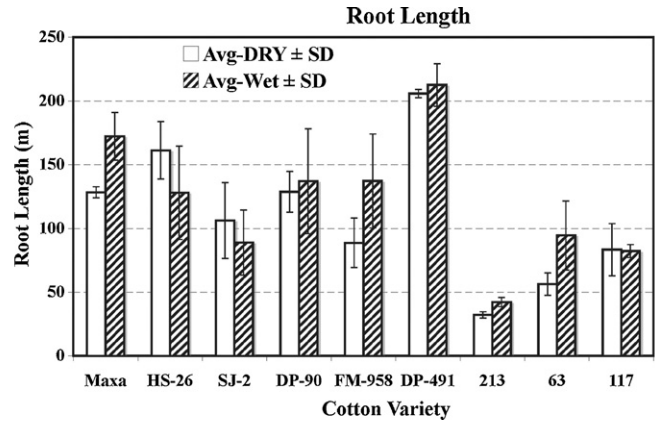


Fig. 5. Average total length of roots ± standard deviation (SD) in wet (white bars) and dry (hatched bars) containers for nine cotton genotypes following HL experiments.

Reports of the total amount of water lifted due to HL ranged from 14% to 33% of the daily ET (Wan et al., 2000; Richards and Caldwell, 1987). Baker and Van Bavel (1988) reported averages of 31% of daily ET that was supplied by water redistributed into dry soil and reabsorbed the following day. Our results indicated that on average 32% was supplied by HL if the daily ET was on the order of 2.0 mm d^{-1}. However, if the daily ET increased threefold to 6 mm d^{-1} (average upper value for Texas High Plains), then only 11% of the total daily ET was supplied by HL. Baker and Van Bavel (1988) reported that the movement of water from the wet to the dry zone through cotton roots was reduced by what they described as disequilibrium in the water potential between the cotton xylem and the surrounding soil when the transpiration was near zero. They postulated that such things as slower equilibration rates between the plant and the soil at lower flow rates or a growth generated water potential change as described by Boyer (1968) may explain the discrepancy between the tissue xylem and soil water potentials.

Other factors such as vertical soil water distribution as well as changes in the root length density profiles may contribute to the degree to which HL directly contributes to daily ET. Baker and Van Bavel (1988) pointed out that the increases in soil water content measured in the dry soil could be the result of root rehydration after root shrinkage occurred during the periods of high transpiration rates as described by Huck et al. (1970). However, as Baker and Van Bavel (1988) explained, evaporative demand was smaller than Huck et al. (1970) experienced in their studies, which could reduce root shrinkage and rehydration. Such could be the case in

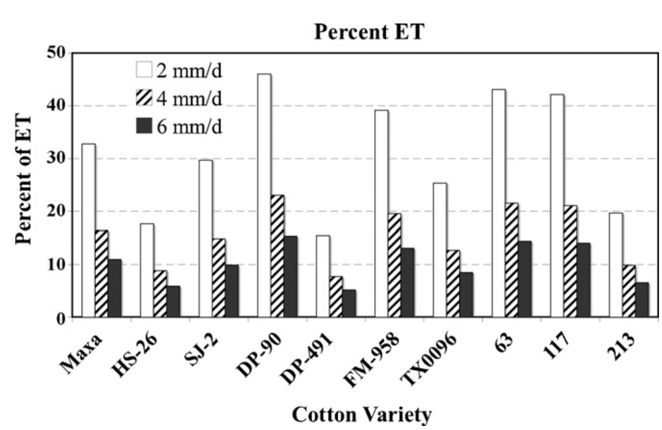


Fig. 6. Percent of daily evapotranspiration (ET) that potentially could be provided by HL for daily ET values of 2, 4 and 6 mm d^{-1}, respectively for each genotype.

our studies since they were carried out in the greenhouse and not in the field as Huck et al. (1970) described.

Changes in RL density, particularly in the upper soil layers, could also contribute to the increased in water redistribution. Wan et al. (2000) showed, for example, that water transfer was observed in drought tolerant lines of corn but not in drought susceptible lines. They stated that differences (increases) in RL density in the upper layers in the drought tolerant lines might have contributed to HL (Wan et al., 2000). In our studies the total RL in the dry side of the containers was always similar or smaller than the RL in the wet side of the system with the exception of the Paymaster HS-26 and Acala SJ-2 varieties (Fig. 5). However, no significant differences were noted in the RL of these two varieties (Data not shown).

The total amount of water that moved into the dry soil in our case was small (Fig. 4). However, when integrated for the soil depth it represents an amount of water that can be important in terms of maintaining the function and lifespan of fine roots near the soil surface to take advantage of short duration high intensity rain events. For example, it has been estimated that for dryland cotton production on the Texas High Plains, 25 mm of rainfall, if made available to the plant, would equate to 25 kg ha^{-1} of additional fiber production (D.R. Krieg, personal communication). Therefore, if root function was maintained to absorb the water from such a rain due to HL, the potential exists for 2800 kg of additional lint production for a 100 ha field. However, additional research is needed to determine the magnitude of HL and if root function is maintained under field conditions before the impact of these phenomena can be quantified across the conditions of the Texas High Plains. The problem is that since we are dealing with small changes in soil water content, it is difficult to measure these changes under field conditions. One approach that has shown promise in both greenhouse studies and under field conditions (Moreira et al., 2003), has been to supply the roots in the lower soil profile with deuterium, a stable isotope of water, and then measure the redistribution of this water in the upper soil profile by collecting water samples for the upper soil and analyzing the samples by mass spectrometer techniques. Again, experimental protocols to determining the extent of HL using this isotopic method must be solved before these techniques can be used in field studies.

5. Conclusions

The results from these studies so far indicated that (1) HL is evident in the germplasm evaluated and (2) the percent of ET derived from the HL ranged from 11% for an ET of 6 mm d^{-1} to 33% for an ET of 2 mm d^{-1}. The amount of water transferred should maintain viable roots near the soil surface to take advantage of water from rain events that in the Texas High Plains are generally of high intensity and short duration. These results are important particularly in dryland cotton production where additional transpiration during the growing season may translate into additional lint yield. Plant breeders may consider this trait in their selection of cotton germplasm with drought resistance.

Acknowledgement

The authors wish to acknowledge Cotton Incorporated (Project No. 05-702) for their continued support of the project.

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